DAILY FOOD CONSUMPTION AND MODE OF INGESTION IN THE HYRAX

By

J.B. SALE
(Zoology Department, University College, Nairobi.)

Introduction

Probably the earliest experiment on hyrax concerned its feeding and was carried out by the 18th Century explorer Bruce, in Ethiopia. He describes (Bruce, 1790) how he shut up a hyrax, which had been starved for a day, in a cage with a chicken. The latter was not eaten by the hungry hyrax. A further experiment involved two small birds which, after several weeks, were also unharmed. From these experiments Bruce concluded that the hyrax was not a carnivore. Most observers agree that hyraces are herbivores and in a recent paper (Sale, 1965a) on the feeding behaviour of rock hyraces, Procavia and Heterohyrax, in Kenya it has been shown that these have catholic dietary habits. A study of the social behaviour of feeding shows rock hyraces to have some patterns similar to the feeding behaviour of ungulates.

The earlier paper emphasised the speed and intensity of feeding in rock hyraces. The total time any colony has been observed group feeding is under one hour per day which, by comparison with many herbivores, is extremely brief. This suggests that either the food consumption of the hyrax is relatively low or that the mode of ingestion permits an unusually rapid rate of food intake. The present paper represents an attempt to elucidate these two factors.

In addition to extensive field observation of feeding colonies, detailed information on the amount eaten and mode of ingestion has been obtained from a captive colony of Mount Kenya hyrax, Procavia johnstoni mackinderi Thomas. For the estimation of food and water intake and the collection of urine and faeces a metabolism cage, to house a single animal, was built (the details of which are being published elsewhere) and kept in a temperature-controlled room.

Amount Eaten.

It is always difficult to assess the amount of food eaten by animals under natural conditions. A certain amount of information can be obtained by weighing the stomach contents of dead animals but this method is unreliable for several reasons. Unless a very large number of animals have been previously examined, it is impossible to state with accuracy the degree to which a stomach is filled. Hence, the contents of what appears to be a full stomach, may in fact represent only half a full meal. In any case, few animals eat the same amount at every meal. Only in rare cases where the behaviour of an animal, for a considerable period prior to death, has been observed, will the exact significance of the stomach contents be known. The method is destructive, uneconomic and denies the possibility of a series of measurements from the same individual, which is essential if any fluctuations are to be recorded. A very large number of "spot" observations of this kind are needed for a given species before a true assessment of the quantity of food it eats can be obtained.

Hyrax in the wild normally have an abundance of food except during rare drought conditions (Sale 1965a). It can thus be assumed that unless some disturbance curtails a feeding period, an animal will eat as much as it requires during each day. An animal that is well settled in captivity and being liberally fed ought, therefore, to give a fairly accurate assessment of the quantitative food requirements of a member of its species of the same age group and sex. A fully adult Mount Kenya male was kept in the metabolism cage and accurate records were maintained of the amount of food put into the cage and the amount uneaten at the end of 24 hours. During the period October 1962 to March 1963, when the room temperature was constant around 21°C (relative humidity varied between 44 and 56%), two contrasting types of food material were given. Freshly-collected sow thistle (*Sonchus sp.*) was fed for the first six weeks and then replaced by lucerne hay. The animal had eaten both these foods equally well during three months in captivity prior to the experimental period. Water-content, nitrogen and crude protein determinations of samples of the food were carried out at intervals and average values for each food over the period obtained. While being fed on *Sonchus*, the animal had no water but was given water *ad lib* while being fed on lucerne. A summary of the data obtained is given in Table I.

It can be seen from Table I that there is a very great difference between the daily intake of *Sonchus* (896 gm) and lucerne (119 gm). This can largely be accounted for by the fact that the former contains much more water (86.6%) than the latter (15.2%). The dry matter intake of the two feeds shows very little difference and appears to be the main factor determining the total amount of food consumed. The much larger quantity of fresh *Sonchus* was apparently not taken in order to obtain water. The urine output decreased significantly when water was mainly obtained through drinking (while feeding lucerne), suggesting that in the first period, water obtained from the *Sonchus* was in excess of requirements. There was also a great increase in the concentration of the urine in the second period, further demonstrating that water was consumed in excess during the first period.

It is clear from these experimental results that the water content of the food greatly influences the amount consumed. Hence the weights of wet stomach contents are a completely unreliable guide to the amount of food being consumed by an animal. If expressed as dry matter, a more useful comparison can be made but will still be subject to the objections stated above.

While the dry matter intake of the two foods was similar, the *Sonchus* provided over 100% more nitrogen and crude protein than the lucerne. Since there was always uneaten lucerne in the cage, it can be assumed that the nitrogen and crude protein provided by the daily intake of this food was adequate. This means that the nitrogen and crude protein provided by the *Sonchus* intake were in great excess of requirements and, like the water provided by the *Sonchus*, were not critical factors in determining the amount of the food consumed. The only factor which shows approximate equality in the two food intakes is the dry matter which must therefore basically determine the amount of a food consumed.

The "voluntary" lowering of the water intake with a lessening of protein intake may reflect a built-in mechanism which cuts down water requirements when the quality of vegetation decreases. Such a protein decrease in the plants takes place during the dry season when water is also short. A mechanism of this kind has recently been demonstrated in native cattle (Payne, 1963) and, if present in hyrax, would partially account for its ability to live for long periods in very arid areas such as the Sahara (Monod, 1963; Grasse, 1956).

The data obtained from this one animal suggest that a large adult male Mount Kenya hyrax will eat approximately 111 gm. (average figure) of dry matter per day. For this animal, weighing 3.3 kg., this is 33.6 gm. per kg. body weight per day. Table 2 compares this ratio with that of other species. The hyrax ratio is in the same range as that of sheep which vary according to body weight, e.g. 31 gm. per kg. body weight for an animal of 79 kg. (Spector, 1956); 34.5 for an animal of 60 kg. (Woodman 1948). This means that for its size the hyrax has a modest food intake, as the ratio normally increases as body weight decreases.

The reason for a relatively low food intake may be that the hyrax is not a very active animal and spends the major part of the day huddled in a hole or lying outside on the rocks (Sale, 1965). It is a marked feature of Table 2 that very active animals such as the Wallaby and Howler Monkey have abnormally high food intakes. Figures could not be obtained for markedly inactive mammals but it seems likely that the converse of the above trend would operate in such cases. An additional factor is that hyrax exhibit a higher degree of thermolability than many mammals (unpublished observation) and will thus use less energy for their size. The low food intake is undoubtedly a significant factor contributing to the ability of the rock hyraces to inhabit areas where vegetation is sparse or of a poor nutritional quality and may also be partially responsible for the fact that they spend relatively little time feeding.

Mode of Ingestion

Use of the feet:

The feet are not extensively used in hyrax for manipulating food. Sometimes a tall herb or small shrub will bear shoots and leaves out of the reach of a feeding animal. If the plant is not stout enough to be climbed, the hyrax may raise itself up and press on the stem about 20 cm. from the ground with its forefeet, thus bending or breaking the stem and bringing the edible parts of the plant within reach. A similar technique is often used by goats and browsing antelopes such as the Gerenuk, *Litocranius walleri* Brooke. If a difficult piece of food is encountered on the ground one of the forefeet may be employed to steady it while a portion is being bitten off. This happens far more frequently in captivity than in the wild. Food such as carrots or mealies which tend to roll around are often held in this way while the side of the mouth is brought into position and a bite taken.

Hyrax have never been observed carrying food into their holes in the wild, although occasionally one finds evidence that a small twig has been dragged into the hole and stripped of its leaves. Even shy newly-captured animals rarely take food into the dark part of the accommodation but generally eat it outside when undisturbed. Mollaret (1962), who has kept both *Procavia* and *Dendrohyrax* in captivity, states that only *Procavia* uses its feet to hold food which it often drags into its shelter to eat there. He does not offer any explanation for the lack of such behaviour in *Dendrohyrax* but it may be connected with the fact that this genus is more easily tamed than *Procavia*, which he admits is the more aggressive and difficult to handle. A tame animal would probably be less afraid of eating in an exposed place than one which was uneasy in captivity. Also Dendrohyrax, being nocturnal, always eats at night.

Unlike many small mammals, hyrax do not pick up objects with their forefeet. The pad-like structure of the feet and absence of really separate prehensile digits (Plate Ib) which make it difficult to do so. The gait of hyrax too, is not predisposed to such action. Mammals, such as many of the rodents, that grasp and lift objects with their hands have long hind limbs on which they are able to walk and sit erect easily, without overbalancing. Although hyrax can stand erect momentarily (tame animals do it when begging for food), they are unable to walk for more than a few steps or sit still in this upright position. The body-shape of the hyrax is similar to that of a bear but the shorter trunk of the latter enables it to balance in the sitting position more easily.

Use of the teeth.

The upper incisors of hyrax are widely separated and developed into a pair of sharp tusks (Plate Ia), triangular in cross-section. The lower incisors, of which there are two pairs, are flattened and deeply incised so as to form comb-like structures used in cleaning the fur, like those of the lemur. Hence the incisors are unsuitable for biting off small shoots and they are little used in ingestion. The normal mode of browsing is to turn the head sideways (at 90° to the body) and bite off the shoot or leaf with the molar teeth and take it in through the side of the mouth (Plate Ic). Hyrax look rather clumsy when feeding and remind one of a carnivore gnawing a large bone which remains projecting from the side of the mouth (Plate Ib). The use of the molars in cropping leads to the distinctive flat-topped appearance of the tussocks of Festuca sp. on Mount Kenya (Plate IIa). Hyrax can be seen with their heads twisted, so as to bring the side of the mouth into a horizontal position during this cropping operation.

The relatively long cutting edge provided by the molars (Plate IIb) enables a large amount of food material to be taken at each bite and thus assists in rapid feeding. The greatest advantage of this will be realised during grazing or cropping when the whole length of the molar row is in use. A rough comparision of the length of the cutting edge and dry matter intake rate in relation to body weight in the hyrax and two grazing ruminants, where the lower incisors form the cutting edge, is given in Table 3 (for authorities see Table 2). It is thus clear that for a herbivore of its size the hyrax can take in food at a very great rate and this must largely account for the relatively brief feeding time.

There is occasional use of the incisor teeth and tongue in ingestion, as follows. If the material is a little out of reach, then, with the neck outstretched, the upper incisors may be used in conjunction with the tongue, the latter pressing the leaf up onto the incisors. The neck is then contracted and as the leaf is pulled, it either breaks along the line of the incisor perforations or it breaks off at the base of its petiole. In the latter case the whole leaf is obtained and can be seen impaled on the upper incisors and projecting from the front part of the animal's mouth. It is removed with the aid of the tongue and the lower incisors.

The lips do not appear to be used in the ingestion of food material but are employed in drinking which strongly resembles that of ungulates. The lips are lowered to just below water level and water is sucked into the mouth in gulps as the lips are slightly parted. The tongue plays very little part in the process.

Rumination and refection.

Ingested food material is rapidly chewed in a side-to-side motion before swallowing. Throughout my observations of rock hyraces I have found no evidence of rumination. Hyrax will sometimes produce a chewing motion without having recently ingested and such action is particularly common when they are confronted by something which is strange to them. It has been observed, for example, when captive animals are introduced to an unfamiliar animal species such as a caged bird. Newly-captured and nervous animals frequently show it when being observed by humans. This motion reminds one forcibly of a ruminant and is probably responsible for the statement by some observers that hyrax chews the cud (Bruce, 1790). Very low intensity pilo-erection is also manifest on such occasions indicating a conflict response to the strange situation (Sale, 1965b).

Recently Hendrichs (1963) claims to have observed rumination in P. capensis in captivity in Europe. He informs me (Hendrichs 1965) that the animals chewed the cud for ½ hr. (in 24 hr.) when fed on dried grass (? hay). Until more details of these observations are available it is unwise to comment but my own view is that although hyrax sometimes chew in the absence of ingestion, they do not regurgitate material from the stomach for further mastication. The simple structure of the stomach would appear to make such action extremely unlikely. Should rumination in the hyrax be established, the accuracy of the Bible (Lev. XI, 5), where the coney is stated to chew the cud, will be attested.

Refection would seem to be a more likely phenomenon in the hyrax than rumination. The process is known to exist in the wild rabbit (Madsen, 1939; Southern 1940,a) and Southern (1940,b) has drawn attention to its possible usefulness during enforced long periods in the burrow due to bad weather or disturbance preventing feeding. Coe (1962) instances a colony of Mount Kenya hyrax that "remained below ground for three days" during a period of bad weather. Although I have no concrete evidence of such prolonged periods without feeding, it seems likely that hyrax can stay in their holes for more than 24 hr. Coprophagy would clearly be a potential mode of nourishment during periods of confinement. Captive hyrax have frequently been seen to sniff and lick fresh faeces but the occurence of actual ingestion has not yet been established. The occurence of refection in the hyrax would provide an interesting comparison with the elephant, where the eating of a quantity of fresh faeces has recently been reported (Dougall and Sheldrick, 1964).

Discussion.

The development of a pair of upper incisors as defensive tusks is one of a number of characteristics that hyrax have in common with the elephant. In both cases this has precluded the use of the incisors for biting and alternative modes of ingestion are used. The elephant has developed the trunk as a highly efficient organ of prehension and suction, unparalled among the mammals. The hyrax have a less unconventional mode of ingestion using the molar teeth, which, because of their long cutting edge allow a large amount of food to be taken in at a time, especially when cropping leafy vegetation. It is interesting that while the elephant is the largest ungulate-type mammal, the hyrax is the smallest. The efficiency of the trunk in ingesting large amounts of food material has undoubtedly contributed to the great size of the modern elephant and enabled the group to radiate out from Africa where it had its origins. The hyraces, on the other hand, have become smaller in size and largely remained confined to Africa where they appear to have had a common origin with the probiscideans in the late Eocene (Romer, 1933). This decrease in size is, however, probably due to the fact that the hyrax has remained plantigrade and has never been capable of the rapid locomotion that enables modern ungulates to escape from predators. Hyraces have therefore left the plains for the protection of rocky outcrops or hollow trees, their sharp incisors being ideal for the defence of the entrance to a hole. This change in niche has necessitated a decrease in size as few existing holes are large enough to house the Oligocene hyraces which were the size of a large hog. Changes in niche and body size have been accompanied by behavioural changes. In general these have involved decreasing activity, resulting in a lowering of relative food requirements.

The survival advantage, to a small herbivore such as hyrax, of a short feeding period, involving maximum exposure to predation, is clear (Sale, 1965a). The factors contributing to the shortness of the feeding time in hyrax, viz a low food intake and rapid mode of ingestion, would seem to have been produced by the physiological and anatomical changes accompanying the change of habit from plains-dwelling grazer to a rock-dwelling browser.

Summary

The dry matter content of a food determines the amount of it that a hyrax will eat. Foods with a low protein content probably demand a lower water intake than those rich in protein. The dry matter intake of an adult Procavia was found to be 33.6 gm per kg. body weight per day, which is low for an animal of this size and may be connected with the relatively inactive life and poor temperature regulation of the rock hyrax.

Hyrax rarely use their feet in grasping food material which is seldom carried into the holes. The development of the incisors for defence and toilet purposes makes them unsuitable for use in ingestion. The molar teeth are used to bite off plant material, an action often necessitating the turning of the head sideways. The cutting edge provided by the molars is relatively long and enables the animal to take in a large amount of food material, thus contributing to the rapid feeding of hyrax.

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Food Consumption in the Hyrax

FOOD	Period in days	Water Content Av. %	DAILY CONSUMPTION IN GM.					
			Av.	Max.	Min.	Dry matter	Nitrogen	Crude protein
Fresh _Sonchus_	39	86.6	896	1940	201	122	3.68	23.08
Lucerne hay	55	15.2	119	280	69	101	1.64	10.28

A summary of food intake data obtained from an adult male (weight 3.3 kg.) Mount Kenya hyrax in the metabolism cage under constant environmental conditions.

TABLE 1.

SPECIES	BODY WT.	Dry matter per kg. body wt. per day
Procavia	3.3 kg.	33.6 gm.
Elephant (African)	3409	29
Zebra (Grevy)	409	20
Wallaby (_M. agilis_)	5	280
Wombat	9	63
Giraffe	1134	28
Howler monkey	3	238
Beef cattle	800	15
Sheep	60	34.5
Rat	0.3	50

A comparison of the daily food (dry matter) intake of various mammals. Compiled from Albritton (1954), Spector(1956) and Woodman (1948).

TABLE 2.

	A. Body Wt.	B. Cutting edge	$\frac{A}{B}$	C. Dry matter per kg. body wt. per day	D. Time spent feeding per day	$\frac{C}{D}$
Procavia	3.3 kg.	3 cm.	1.1	33.6 gm.	.66 hr.	50.8,
Sheep	79	3	26	31	10.5	2.95
Cow	800	8	100	15	6.5	2.3

TABLE 3.

<u>Plate Ia</u> The incisor teeth of a male hyrax. The lower incisors of this old animal are worn down to peg-like stumps and are no longer comb-like.

<u>Plate Ib</u> An animal eating a leaf which remains projecting out of the side of the mouth. The peculiar form of the feet can also be seen.

<u>Plate Ic</u> Browsing hyrax, showing how the head is turned sideways as vegetation is bitten off with the molars.

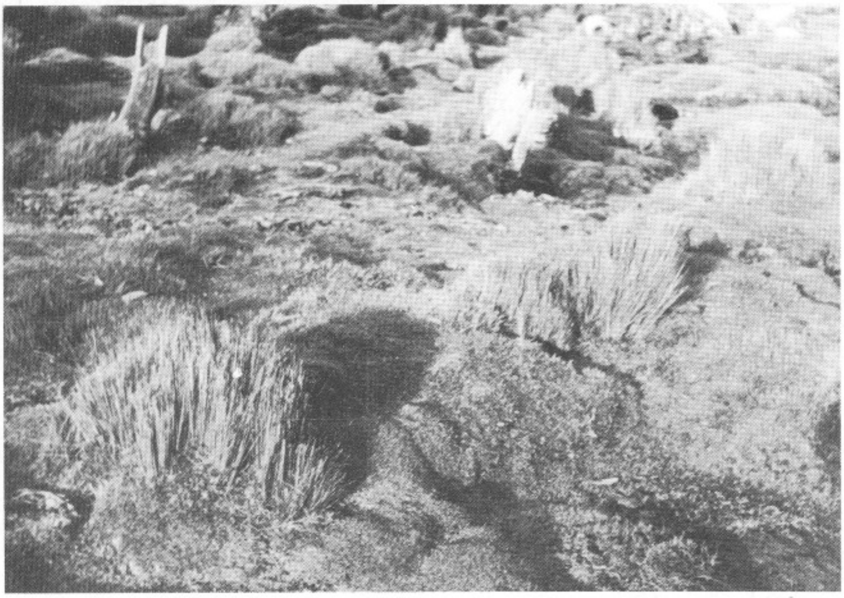

Plate IIa Tussocks on Mount Kenya that have been cropped by hyrax, resulting in a characteristic flat-topped appearance.

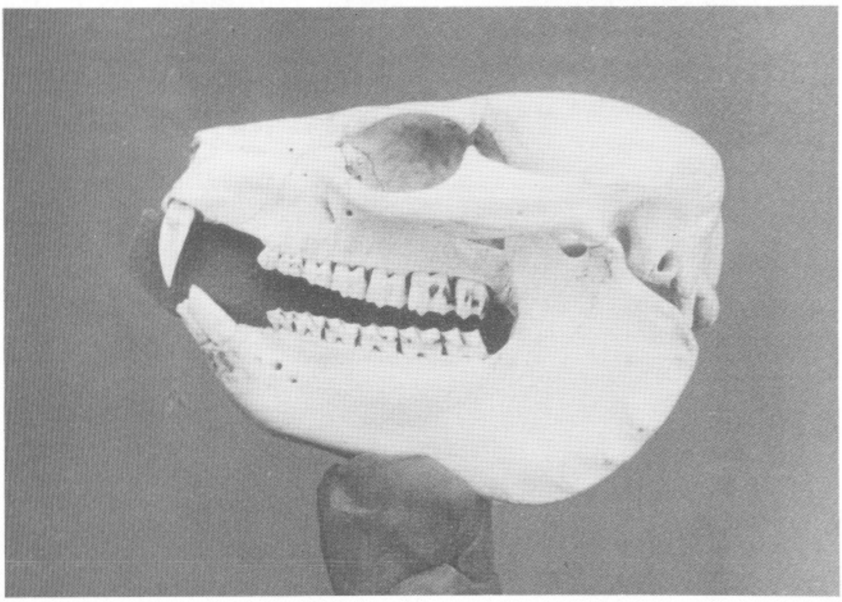

Plate IIb A skull from the side showing molar teeth. The outer cutting edge of the upper molars overlaps the narrower lower molars when the jaws close,thus producing a scissors action.